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Effects of soil pasteurisation and soil N status on severity of *Striga hermonthica* (Del.) Benth. in maize

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Abstract

The nature of interrelationships between soil pasteurisation, and increased soil N content, on the severity of *Striga hermonthica* infection in maize was studied in pot experiments in the screen-house. An initial experiment revealed that there was no significant difference in amount of *S. hermonthica* infection in maize grown in potted soil collected from Bida (9°05′N, 6°01′E) and Ibadan (7°17′N, 3°30′E). However, there was 57% increase in amount of *S. hermonthica* infection and a 68% reduction in maize shoot dry matter when maize was grown in pasteurised soil compared with natural soil. In another experiment, soil steaming significantly influenced the effects of increased soil N fertility (from preceding soybean cv. SAMSOY-2 or application of 90 kg N ha^{-1}) on severity of *S. hermonthica* in maize. In natural soil, application of N to maize reduced (by 53%) the number of emerged *S. hermonthica* plants and increased (by 154%) maize dry matter compared with no fertilizer application. In pasteurised soil, application of N to maize increased *S. hermonthica* severity by 26% and also significantly increased maize dry matter compared with no fertilizer application. The same effects were observed when soybean was used to increase soil N content. Analysis of natural and pasteurised soil revealed only minor differences in composition of K^+, Na^+, Cu, Mn, and Fe, and none of these changes was directly related to *S. hermonthica* infection in maize. Results of this study indicate that the differences in *S. hermonthica* infection in pasteurised and natural soil could be attributed to soil biotic factors that reduce *S. hermonthica* infection in natural soil. The results partly provide an explanation for the wide variation in reports on the effects of N fertilization on severity of *S. hermonthica* infection and stress the need for understanding the mechanisms of natural reduction in *S. hermonthica* infection and interactions of these natural mechanisms with other control techniques.

Keywords: *Striga hermonthica*; Soil suppressiveness; N fertility; Integrated *Striga* management

1. Introduction

Flowering plant species of the genus *Striga* (Scrophulariaceae) are obligate root parasites that are major constraints to cereal and legume production in the savannas of Africa (Musselman, 1987; Emechebe et al., 1991). *Striga hermonthica* (Del.) Benth., the most important parasitic seed plant on a global scale (Parker and Riches, 1993), is endemic in the African savannas, where it causes severe losses in mostly cultivated cereal crops, thereby adversely affecting the lives of over 100 million African people (Mboob, 1989).

Intensification of land use, reflected in intensive cereal mono-cropping with little or no fallow to non-host crops, has contributed to increased *Striga* problem in Africa (Berner et al., 1995; 1996a,b). Effective control of the parasite is difficult because of its small sized seed with longevity up to 14 years, high reproductive capacity (10,000–100,000 seeds per plant), and complex parasite-host relationship (Saunders, 1933; Bebawi et al., 1984; Ejeta et al., 1993). In addition, the parasite causes up to 75% of its overall damage to the host during the underground stage of development, emerging usually after the last weeding has been effected (Parker and Riches, 1993). Consequently,

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control targeted at only emerged *Striga* plants frequently does not result in increased host yield. Recent efforts focus on developing integrated *S. hermonthica* management options such as legume rotation, use of host-plant resistance, and soil-based biological control (Berner et al., 1996b).

The existence of natural biotic soil suppressiveness to *S. hermonthica* has been suggested by Berner et al. (1996b) based on their study of soil samples from 11 locations in Nigeria. Results of their study strengthened an earlier suspicion by Parker and Riches (1993) that soil-borne pathogens of *Striga* may suppress it naturally in some soils. The demonstration of existence of biotic suppression to *S. hermonthica* by Berner et al. (1996b) led to the question of how to manage soils and crops to maximise suppressiveness to *S. hermonthica.*

Control of *S. hermonthica* through application of nitrogenous fertilizers and organic matter amendments has been intensively studied, often with varying and contradictory results from different locations. Particularly, N fertilization has been reported to reduce incidence of *Striga* spp. infection (Farina et al., 1985; Kim and Winslow, 1992; Igbinnosa et al., 1996), while others (Osman et al., 1991; Smaling et al., 1991; Gworgwor, 1993) have reported that N fertilization had either no effect or resulted in increased parasitism by *Striga* spp. However, none of these studies related N fertilization to the level of inherent biotic soil suppressiveness. In this study, we investigated in pot experiments, possible interrelationships between soil biota, improved soil N fertility through legume rotation or through inorganic N fertilizer, and the severity of *S. hermonthica* in maize.

2. Materials and methods

2.1. Effect of soil pasteurisation on severity of S. hermonthica infection in maize

A pot experiment was conducted in the screenhouse at the International Institute of Tropical Agriculture, Ibadan, Nigeria (IITA) from September to December 1998 to determine if soil sterilisation (as a technique for eliminating biotic suppression of *S. hermonthica*) results in increased infection by the parasite. Soil samples used for this experiment were obtained from the high root-density zone of natural savanna vegetation in Bida, Nigeria (9°05′N, 6°01′E), and from secondary forest in Ibadan, Nigeria (7°17′N, 3°30′E). Plastic pots (18 cm diameter, 17.5 cm depth, perforated at the bottom) were filled with 4 kg of soil. To pasturise the soil, pots containing soil were loaded in a motorised chamber, closed and connected to an aerated steaming machine (Model 'SF' Burner, MP 1192, R.W. Beckett Corp., Elyria, OH, USA) and steamed for 4 h. *S. hermonthica* seeds were collected from parasite plants attacking sorghum (*Sorghum bicolor* L.) in farmers' fields at Bida, Nigeria in November 1996. The seeds were air-dried in the screenhouse at IITA, sieved, cleaned and stored in polyethylene containers at ambient temperature in the laboratory at IITA. Soil in each pot was infested with approximately 3000 (0.05 g) germinable-*S. hermonthica* seeds by thoroughly mixing the top 5 cm layer of soil with *S. hermonthica* seeds. The pots were watered necessarily (in order to avoid moisture stress) for one week to condition the parasite seeds before planting maize (Worsham, 1987). After 1 week, four seeds of *S. hermonthica* susceptible maize (cv. 8338-1) were planted in each pot, and resulting plants were thinned, 1 week-after-planting (WAP), to one plant per pot.

The experimental treatments were, original location of soil sample (Bida and Ibadan) and soil pasteurisation (pasteurised soil and natural soil). The experimental layout was a randomised complete block design (RCBD) with each treatment replicated five times.

Data collected included emerged *S. hermonthica* plants counted weekly (starting from the time of first parasite emergence until harvest at 12 WAP), and aboveground maize dry-weight. At 12 WAP, maize shoots were cut just above the soil level, oven dried for 72 h at 80 °C and weighed.

2.2. Effects of interaction between soil pasteurisation, the crop preceding maize and application of inorganic N to maize on severity of infection by S. hermonthica

This pot experiment was conducted at IITA, from March to July 1999. A soil sample collected from Ibadan (described in Section 2.1) was used. Plastic pots (described in Section 2.1) were filled with 4 kg of soil. One half the total number of potted soil was planted to promiscuously nodulating soybean (cv. SAMSOY-2), and the other half to maize (cv. 8338-1). Two soybean plants or one maize plant were maintained per pot. At 3 WAP, NPK (15:15:15) fertilizer was applied to all the pots at a rate of 30 kg NPK ha^{-1} (0.36 g NPK fertilizer pot^{-1}). All the pots contained natural soil without *S. hermonthica* seeds. At 10 WAP, the plants (both soybean and maize) were harvested, and one half of the pots that were planted to soybean and maize were pasteurised as described in Section 2.1, the other half was not. All the pots were then infested with *S. hermonthica* seeds at approximately 3000 germinable seeds per pot, and the soil was kept moist for one week to condition the parasite seeds before planting maize (cv. 8338-1). At 1 WAP, half the pots were fertilized with 90 kg N ha^{-1}(0.36 g urea pot^{-1}); the remaining half that did not receive N fertilizer served as a control. The experimental layout was an RCBD in 2^3 factorial, i.e. preceding crop = soybean or maize; soil pasteurisation = pasteurised or natural soil; N fertilizer = 90 or 0 kg N ha^{-1}, with five replications per treatment. Data collected were the same as described in Section 2.1.

2.3. Soil analyses

Pasteurised and natural samples of soil collected from secondary forest at IITA, were analysed for soil chemical properties to find out those properties that may change with pasteurisation and that are likely to relate to suppression of *S. hermonthica* in natural soil. Samples were collected and prepared for analysis 2 days after pasteurisation, while the analysis was done 1 week after pasteurisation. The individual samples of the pasteurised and natural soil were air-dried and ground to pass through a 2 mm sieve; duplicate samples for organic carbon and total percentage of nitrogen determination were further pulverised to pass through a 0.5 mm sieve. Soil chemical analysis was carried out at IITA following the routine procedures for soil analysis described by Juo (1981). Soil pH, organic carbon (%), total nitrogen (%), carbon/nitrogen ratio, Bray-1 P (mg/kg), exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}, Mn^{2+}), effective CEC, and micro-nutrients (Cu, Zn, Mn, Fe) were determined.

2.4. Statistical analysis

Data were analysed by the Mixed Model procedure in SAS (Littell et al., 1996) taking replication and treatments as random and fixed effects, respectively. To determine levels of significance associated with differences in means of number of emerged *S. hermonthica* plants, square root transformed data were used in the statistical analysis. Orthogonal contrasts were made to test differences between specific treatment means.

3. Results

3.1. Effect of soil pasteurisation on incidence of S. hermonthica in maize

Emergence of *S. hermonthica* in maize started at 4 WAP and weekly counts of emerged *S. hermonthica* plants were significantly ($P \leq 0.05$) greater in pasteurised soil from 6 WAP up to harvest at 12 WAP, compared with the natural soil from both Bida and Ibadan (Fig. 1). The greatest number of emerged *S. hermonthica* plants occurred in pasteurised soil from Bida (12.2 plants pot^{-1}) and Ibadan (12 plants pot^{-1}) at 10 WAP, while the corresponding data in natural soil from Bida (5.7 plants pot^{-1}) and Ibadan (5.1 plants pot^{-1}) occurred at 8 WAP (Fig. 1).

The number of emerged *S. hermonthica* did not differ significantly between the two soils, but maize dry-weight was significantly ($P \leq 0.1$) greater in Ibadan soil than in Bida soil (Table 1). On the other hand, soil pasteurisation significantly ($P \leq 0.01$) affected number of emerged *S. hermonthica* plants and associated maize dry-weight (Table 1). Across locations, the number of emerged *S. hermonthica* plants and maize dry-weight were 56.5% higher and 68.4% lower, respectively, in pasteurised than in natural soil. In the Bida soil, the number of emerged *S. hermonthica* in maize was 51.5% higher ($P \leq 0.1$) and maize shoot dry-weight 71.7% lower ($P \leq 0.05$) in pasteurised soil than in natural soil (Table 1). Similarly, in Ibadan soil, the number of emerged *S. hermonthica* was 61.4% higher ($P \leq 0.05$) and maize shoot dry-weight 66% lower in pasteurised than in natural soil (Table 1).

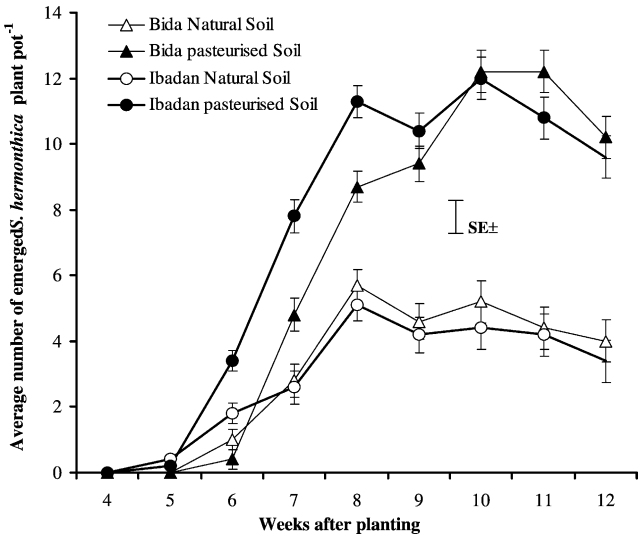

Fig. 1. Effect of soil pasteurisation on weekly emergence of *S. hermonthica* from soil from Bida and Ibadan in pot culture at IITA, Ibadan, 1998.

3.2. Effects of interaction between soil pasteurisation, the crop preceding maize and application of inorganic N to maize on severity of infection by S. hermonthica

The effects of soil pasteurisation, crop preceding maize (soybean or maize), and inorganic N fertilizer application to maize on the severity of *S. hermonthica* infection (as measured by number of emerged *S. hermonthica* plants) were significant. Effects of all the three factors on maize shoot dry-weight were also significant. Interactions between soil pasteurisation and the crop preceding maize and between soil pasteurisation and N fertilization were each significant ($P \leq 0.05$) for number of emerged parasite plants. Similarly, the three-way interaction of soil pasteurisation, the crop preceding maize and N fertilization was also significant ($P \leq 0.1$). The interactions between soil pasteurisation and the crop preceding maize, as well as that between the crop preceding maize and N fertilization, were significant ($P \leq 0.001$) for maize shoot dry-weight.

There were significantly higher number of emerged *S. hermonthica* plants, accompanied by lower maize shoot dry-weight in pasteurised soil than in natural soil (Table 2). In pasteurised soil, there was no significant difference between number of emerged *S. hermonthica* in maize grown after maize and that in maize grown after soybean, however, maize shoot dry-weight was higher

Table 1
Number of emerged *S. hermonthica* plants in maize (var. 8338-1) and maize shoot dry-weight in potted pasteurised and natural Bida and Ibadan soils in screenhouse pot experiment at IITA, Ibadan (September–December 1998)

Treatment	Number of emerged *S. hermonthica* pot^{-1}[a]			Maize shoot dry-weight (g) pot^{-1}		
	Mean	Estimated difference (%)[b]	SE ±	Mean	Estimated difference (%)[b]	SE ±
Location of soil sample						
Bida	10.1 (3.1)	4.0	(0.41)	12.8	−28.8*	2.06
Ibadan	9.7 (3.0)			16.5		
Soil pasteurisation						
Pasteurised soil	13.8 (3.7)	56.5***	(0.41)	10.9	−68.4***	2.06
Natural soil	6.0 (2.4)			18.3		
Location-soil pasteurisation						
Bida-pasteurised soil	13.6 (3.7)	51.5*	(0.58)	9.4	−71.7**	2.92
Bida-natural soil	6.6 (2.6)			16.1		
Ibadan-pasteurised soil	14.0 (3.6)	61.4**	(0.58)	12.4	−65.9***	2.92
Ibadan-natural soil	5.4 (2.3)			20.5		

[a] Values in parenthesis are $\sqrt{(X+0.05)}$ transformed.
[b] Prob. $> t$, *significant at $P \leq 0.1$, **significant at $P \leq 0.05$, ***significant at $P \leq 0.01$.

($P \leq 0.01$) when maize followed soybean than when it followed maize (Tables 2 and 3). In natural soil, the number of emerged *S. hermonthica* in maize grown after soybean was lower ($P \leq 0.001$) with a corresponding higher ($P \leq 0.001$) maize shoot dry-weight compared with maize grown after maize (Tables 2 and 3).

Similarly, in pasteurised soil, application of 90 kg N ha^{-1} to maize significantly ($P \leq 0.001$) increased the number of emerged *S. hermonthica* by 26%, though maize dry-weight still increased significantly by 106% compared with maize without fertilizer (Tables 2 and 3). On the contrary, in natural soil, application of urea (at 90 kg N ha^{-1}) resulted in 53% reduction in number of emerged *S. hermonthica* plants ($P \leq 0.001$) and 154% increase in maize shoot dry-weight ($P \leq 0.001$) compared with no fertilization (Tables 2 and 3). The results also showed that in natural soil, N fertilization reduced number of emerged *S. hermonthica* and increased maize shoot dry-weight significantly (Tables 2 and 3), irrespective of preceding crop.

Table 2
Number of emerged *S. hermonthica* plants in maize and shoot dry-weight of maize (cv. 8338-1) grown with or without N fertilization application in pasteurised or natural soil previously cropped to soybean (cv. SAMSOY-2) or maize (var. 8338-1)

Treatment	Number of emerged *Striga* pot^{-1}									
	Natural soil				Pasteurised soil				Mean[2]	SE ± [2]
	Preceding crop		Mean[1]	SE ± [1]	Preceding crop		Mean[1]	SE ± [1]		
	Maize	Soybean			Maize	Soybean				
0 kg N ha^{-1}	26.8 (5.2)	13.8 (3.8)	20.3 (4.6)	(1.22)	29.0 (5.4)	28.0 (5.3)	28.5 (5.4)	(1.22)	24.4 (5.0)	(0.87)
90 kg N ha^{-1}	12.4 (3.6)	6.6 (2.7)	9.5 (3.2)		34.6 (5.9)	37.2 (6.1)	35.9 (6.0)		22.7 (4.8)	
Mean[3]	19.6 (4.5)	10.2 (3.3)	14.9 (3.9)		31.8 (5.7)	32.6 (5.8)	32.2 (5.7)		23.6 (4.9)	
SE ± [3]					(1.22)					
Mean maize shoot dry-weight (g) pot^{-1}										
0 kg N ha^{-1}	3.3	13.3	8.3	1.01	2.7	5.7	4.2	1.01	6.3	0.84
90 kg N ha^{-1}	16.7	25.6	21.1		7.1	10.2	8.7		14.9	
Mean[3]	10.0	19.4	14.7		4.9	8.0	6.4		10.6	
SE ± [3]					1.01					

Values in parenthesis are $\sqrt{(X+0.05)}$ transformed. Mean[1] = means within soil, Mean[2] = means across soil, Mean[3] = means across fertilizer rates, SE ± [1] = SE ± for comparing preceding crop within fertilizer and soil, SE ± [2] = SE ± for comparing soil within and across fertilizer rates, SE ± [3] = for comparing fertilizer within and across crop and soil.

Table 3
Specific contrasts of number of emerged *S. hermonthica* plants in maize and shoot dry-weight of maize (cv. 8338-1) grown with or without N fertilization in pasteurised or natural soil previously cropped to soybean (cv. SAMSOY-2) or maize (cv. 8338-1)

Treatment contrast	Estimated difference (%)[a]	
	Number of emerged *Striga* plants pot^{-1}	Maize shoot dry-weight (g pot^{-1})
Soybean × natural soil vs maize × natural soil	−48.0****	+93.9****
Soybean × pasteurised Soil vs maize × pasteurised Soil	+2.5	+62.1***
90 kg N ha^{-1} × natural soil vs 0 kg N ha^{-1} × natural soil	−53.2****	+154.0****
90 kg N ha^{-1} × pasteurised soil vs 0 kg N ha^{-1} × pasteurised soil	+26.0****	+105.7****
Maize × 90 kg N ha^{-1} × natural soil vs maize × 0 kg N ha^{-1} × natural soil	−53.7****	+400.0****
Soybean × 90 kg N ha^{-1} × natural soil vs soybean × 0 kg N ha^{-1} × natural soil	−52.2***	+92.2****
Maize × 90 kg N ha^{-1} × pasteurised soil vs maize × 0 kg N ha^{-1} × pasteurised soil	+19.3**	+160.7***
Soybean × 90 kg N ha^{-1} × pasteurised soil vs soybean × 0 kg N ha^{-1} × pasteurised Soil	+32.9****	+79.4***

[a] Prob. > t, *significant at $P \leq 0.1$, **significant at $P \leq 0.05$, ***significant at $P \leq 0.01$, ****significant at $P \leq 0.001$.

3.3. Soil analyses

Table 4 shows the chemical properties of natural, and pasteurised samples of soil collected from secondary forest in IITA, Ibadan. Only K^+, Na^+, Cu, Mn, and Fe showed any appreciable differences between non-sterile and steam-sterilised soil. None of these differences directly correlated with number of emerged *S. hermonthica* at $P \leq 0.1$.

4. Discussion

The observed greater severity of *S. hermonthica* infection in maize grown in pasteurised soils than in natural soils (Tables 1–3) throughout this study suggest that some changes in pasteurised soils make them more conducive for maize infection by *S. hermonthica* compared with natural soils. Previously, Berner et al. (1996b) studied *S. hermonthica* infection in soil samples from 11 locations in Nigeria and found an overall reduction of 47% ($P < 0.01$) in number of *S. hermonthica* attached to maize in natural soil compared with pasteurised samples of the soils. Findings of the present study confirm those of Berner et al. (1996b) who attributed the differences to the existence of suppressiveness to *S. hermonthica* in natural (unpasteurised) soil, but not in pasteurised soil. They proposed that the difference in *S. hermonthica* parasitism between natural and pasteurised soil was probably microbial in origin, microorganisms having been eliminated from the soil by pasteurisation process. This agrees with the microbial origin of well-studied suppressive soils for some diseases (Baker and Cook, 1974; Scher and Baker, 1980; Schroth and Hancock, 1982; Lumsden et al., 1987).

Table 4
Chemical composition of natural and pasteurised (4 h steaming) soil samples collected from secondary forest at IITA, Ibadan

Soil chemical property	Natural soil	Pasteurised soil
pH (H_2O) (1:1)	5.50 ± 0.02	5.60 ± 0.05
Organic carbon C (%)	0.99 ± 0.06	0.90 ± 0.03
Kjeldahl nitrogen N (%)	0.13 ± 0.03	0.12 ± 0.03
C-to-N ratio	7.60 ± 2.0	7.50 ± 2.70
Bray-1 P (mg kg^{-1})	5.40 ± 0.20	4.60 ± 0.30
Exchangeable Ca (cmol$_{(+)}$ kg^{-1})	8.30 ± 0.61	8.80 ± 0.53
Exchangeable Mg (cmol$_{(+)}$ kg^{-1})	0.90 ± 0.04	0.80 ± 0.07
Exchangeable K (cmol$_{(+)}$ kg^{-1})	0.20 ± 0.06	0.30 ± 0.03
Exchangeable Na (cmol$_{(+)}$ kg^{-1})	0.30 ± 0.05	0.20 ± 0.03
Exchangeable Mn (cmol$_{(+)}$ kg^{-1})	0.20 ± 0.01	0.20 ± 0.02
Effective CEC (cmol$_{(+)}$ kg^{-1})	9.70 ± 1.20	10.10 ± 0.91
Cu (ppm)	1.80 ± 0.12	2.60 ± 0.18
Zn (ppm)	3.50 ± 0.20	3.30 ± 0.20
Mn (ppm)	34.60 ± 3.67	27.0 ± 2.53
Fe (ppm)	20.20 ± 2.10	16.0 ± 1.55

Although, changes in some physical–chemical properties of the soil following pasturisation may contribute to greater *S. hermonthica* severity in pasteurised soil, no direct correlation was found in this study between change in mineral nutrients (Fe, Mn, Cu, Na^+ and K^+) and maize parasitism by *S. hermonthica*. Hence, the higher incidence of *S. hermonthica* in pasteurised compared to natural soil in this study, is attributable to *S. hermonthica* suppressing biotic factors in the natural soil, which were eliminated or negatively affected by pasteurisation.

The results of this study further showed that *S. hermonthica* emergence was significantly reduced in maize grown after soybean in natural soil (Tables 2 and 3). Soil infestation with *S. hermonthica* seeds in this study was done after soybean harvest, before planting the bioassay maize. Hence, the reduction in number of emerged *S. hermonthica* plants in this study was independent of the ability of soybean varieties, such as SAMSOY-2, to deplete *S. hermonthica* seed population in soil through suicidal germination (Berner et al., 1995, 1996b; Carsky et al., 2000). Rather, the suppression is attributable to the soil N increasing ability of soybean (Peoples et al., 1995; Carsky et al., 1997) and increased availability of nutrients other than N through

increased soil microbial activity during the legume crop (Kucey et al., 1988; Wani et al., 1995). It is therefore suggested that breeding legumes for rotation with cereals to control *S. hermonthica* should focus on both enhanced soil fertility and suicidal germination of the parasite.

Reduced *S. hermonthica* emergence in natural soil as a result of application of N fertilizer (Tables 2 and 3) agrees with reports of several previous workers (Farina et al., 1985; Kim and Winslow, 1992; Igbinnosa et al., 1996). Conversely, several other workers (Osman et al., 1991; Smaling et al., 1991; Gworgwor, 1993) have reported either no effect or stimulatory effect of N fertility on *Striga* spp. emergence. However, none of these works has been related to a possible interaction with natural biotic soil suppression of *Striga* spp. In the study reported here, increased availability of soil N increased the severity of *S. hermonthica* in pasteurised soil, while in natural soil, increased soil N status resulted in significant reductions in infection by *S. hermonthica* (Tables 2 and 3). The results suggest that reduction of *S. hermonthica* parasitism as a result of increase in soil N in natural soil is associated with the existence of biotic factors in such soils, which are improved by increasing N availability. The implication may be that in fields where such biotic factors do not operate or exist, application of nitrogenous fertilizers, organic matter, or other cultural practices aimed at improving soil fertility, may have no immediate effect on reducing *S. hermonthica* infection. This may partly explain contradictions in reports on the effect of N on *Striga* spp. severity.

Results indicate that soil suppressiveness to *S. hermonthica* (sensu Berner et al., 1996b) exists and that it is biotic. Natural biotic soil suppressiveness is an important factor that needs consideration in integrated *S. hermonthica* management because of its potential interactions with cultural practices such as N fertilizer application and legume rotation aimed at controlling the parasite. There is need for further studies to elucidate the mechanisms of biotic suppression of *S. hermonthica* infection in natural soil and its interaction with other soil factors, in formulating a sustainable integrated management practice for the parasite.

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References

Baker, K.F., Cook, R.J., 1974. Biological Control of Plant Pathogens, W.H. Freeman, San Francisco, 433 p.

Bebawi, F.F., Eplee, R.E., Harris, C.E., Norris, R.S., 1984. Longevity of witchweed (Striga asiatica) seed. Weed Science 32, 494–497.

Berner, D.K., Kling, J.G., Singh, B.B., 1995. Striga research and control: a perspective from Africa. Plant Disease 79, 652–670.

Berner, D.K., Alabi, M.O., Di-Umba, U., Ikie, F.O., 1996a. Proposed integrated control program for *Striga hermonthica* in Africa. In: Moreno, M.T., Cubero, J.I., Berner, D., Joel, D., Musselman, L.J., Parker, C. (Eds.), Advances in Parasitic Plant Research, Proceedings of the Sixth Parasitic Weeds Symposium, April 16–18, 1996, Junta de Andalucia, Direccion General de Investigacion Agraria, Cordoba, Spain, pp. 817–825.

Berner, D.K., Carsky, R., Dashiell, K., Kling, J.G., Manyong, V.M., 1996b. A land management based approach to integrated *Striga hermonthica* control in sub-Saharan Africa. Outlook on Agriculture 25 (3), 157–164.

Carsky, R.J., Abidoo, R., Dashiell, K., Sanginga, N., 1997. Effect of soybean on subsequent maize grain yield in the guinea savanna zone of West Africa. African Crop Science Journal 5 (1), 31–38.

Carsky, R.J., Berner, D.K., Oyewole, B.D., Dashiell, K., Schulz, S., 2000. Reduction in *Striga hermonthica* parasitism on maize using soybean rotation. International Journal of Pest Management 46 (2), 115–120.

Ejeta, G., Butler, L.G., Babiker, A.G.T., 1993. New Approaches to the Control of *Striga*, Research Bulletin no. 991, Purdue University Agricultural Experiment Station, West Lafayette, Indiana, USA, 27 p.

Emechebe, A.M., Singh, B.B., Leleji, O.I., Atokple, I.D.K., Adu, J.K., 1991. Cowpea-*Striga* problem and research in Nigeria. In: Kim, S.K., (Ed.), Combating *Striga* in Africa, Proceedings, International Workshop Organized by IITA, ICRISAT and IDRC, 22–24 August 1988, IITA Ibadan, Nigeria, 1988., pp. 18–28.

Farina, M.P.W., Thomas, P.E.L., Channon, P., 1985. Nitrogen, phosporus and potassium effects on the incidence of *Striga asiatica* (L.) Kuntze in maize. Weed Research 25 (6), 443–447.

Gworgwor, N.A., 1993. Studies on the biology and control of Striga species (Scrophulariaceae). Inaugural-Dissertation, Fachbereichs Biologie der Philipps-Universität, Marburg. 184 p.

Igbinnosa, I., Cardwell, K.F., Okonkwo, S.N.C., 1996. The effect of nitrogen on the growth and development of giant witchweed, *Striga hermonthica* Benth.: effect on cultured germinated seedlings in host absence. European Journal of Plant Pathology 102, 77–86.

Juo, A.S.R., 1981. Automated and Semi-automated Methods for Soil and Plant Analysis, Manual Series No. 7, International Institute of Tropical Agriculture, Ibadan, Nigeria.

Kim, S.K., Winslow, M.D., 1992. Breeding maize for *Striga* resistance. IITA Research 4, 9–12.

Kucey, R.M.N., Chaiwanakupt, P., Arayangkool, T., Snitwongse, P., Siripaibool, C., Wadisirisuk, P., Boonkerd, N., 1988. Nitrogen fixation (^{15}N dilution) with soybeans under Thai field conditions. II. Effect of herbicides and water application schedule. Plant and Soil 108, 87–92.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS© System for Mixed Models, SAS Institute Inc. USA, Cary NC, 633 p.

Lumsden, R.D., García-E, R., Lewis, J.A., Frías-T, G.A., 1987. Suppression of damping-off caused by *Pythium* spp. in soil from the indigenous Mexican chinampa agricultural system. Soil Biology & Biochemistry 19, 501–508.

Mboob, S.S., 1989. A regional program for West and Central Africa. In: Robson, I.O., Broad, H.R. (Eds.), *Striga*—Improved Management in Africa, Proceedings, FAO/OAU All-Africa Government Consultation on Striga Control, pp. 190–194, Maroua, Cameroon.

Musselman, L.J. (Ed.), 1987. Parasitic Weeds in Agriculture, Striga, vol. I. CRC Press, Boca Raton, p. 317.

Osman, M.A., Raju, P.S., Peacock, J.M., 1991. The effect of soil temperature, moisture and nitrogen on *Striga asiatica* (L.) Kuntze seed germination, viability and emergence on sorghum (*Sorghum bicolor* (L.) Moench.) roots under field conditions. Plant and Soil 131, 265–273.

Parker, C., Riches, C.R., 1993. Parasitic Weeds of the World: Biology and Control, CAB International, Wallingford, UK, 332 p.

Peoples, M.B., Herridge, D.F., Ladha, J.K., 1995. Biological nitrogen fixation: an efficient source of nitrogen for sustainable agriculture production? Plant and Soil 174, 3–28.

Saunders, A.R., 1933. Studies in Phanerogamic parasitism, with particular reference to *Striga lutea* Lou. South Africa Department of Agriculture, Science Bulletin 128, 56p.

Scher, F.M., Baker, R., 1980. Mechanism of biological control in a *Fusarium*-suppressive soil. Phytopathology 70, 412–417.

Schroth, M.N., Hancock, J.G., 1982. Disease-suppressive soil and root-colonizing bacteria. Science 216, 1376–1381.

Smaling, E.M.A., Stein, A., Sloot, P.H.M., 1991. A statistical analysis of the influence of *Striga hermonthica* on maize yields in fertilizer trials in southwestern Kenya. Plant and Soil 138 (1), 1–8.

Wani, S.P., Rupela, O.P., Lee, K.K., 1995. Sustainable agriculture in the semi-arid tropics through biological nitrogen fixation in grain legumes. Plant and Soil 174, 29–49.

Worsham, A.D., 1987. Germination of witchweed seeds. In: Musselman, L.J., (Ed.), Parasitic Weeds of Agriculture, Striga, 1. CRC Press, Boca Raton, FL, pp. 45–62.